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Global warming effects on yield and fruit maturation of olive trees growing under field conditions

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ABSTRACT

Temperature in the Mediterranean Basin, the main area of olive (*Olea europaea* L.) cultivation, has been projected to rise drastically in the near future threatening olive production. To determine the potential effects of higher temperature on the olive fruiting cycle and vegetative growth, a study with the cultivar 'Picual' has been carried out simulating global warming conditions under field conditions. Temperature-controlled open top chamber (OTC) systems were used to increase the day/night ambient temperature 4 °C throughout the complete reproductive cycle of this species. Three years of study have shown that 4 °C increase of ambient temperature reduces fruit yield and affects fruit characteristics and maturation processes. Smaller fruits, lower pulp/stone ratio, oil yield and anthocyanin contents were observed. The maturation period was forwarded and extended in trees subjected to warmer temperatures. In addition, the vegetative growth was stimulated by the temperature treatment resulting in trees of bigger size.

1. Introduction

The Mediterranean Basin is the largest area in the world with a specific climate for olive (*Olea europaea* L.) cultivation. However, the environmental conditions of this region are expected to change in the near future (Giorgi, 2006). In particular, the mean air temperature has been projected to rise drastically in the range of 2–5 °C (Giorgi, 2006; Giannakopoulos et al., 2009; Gualdi et al., 2013; IPCC, 2014). In addition, more heatwave days and tropical nights and an extension of the dry season will be observed (Giannakopoulos et al., 2009).

Olive production depends on vegetative and reproductive processes occurring along a biennial cycle. Both processes are repeated annually, but while shoot growth is completed within the same year, processes leading to fruit bearing require two consecutive seasons. Briefly, in the first one, buds are formed in the leaf axils of growing shoots and flowers are induced. After floral bud dormancy, during the second season, inflorescences and flowers develop until flowering, and then fertilization and fruit set occur. In the next stage, fruits develop and grow until ripening (Rallo and Cuevas, 2008). All these processes are regulated, among other factors, by climate conditions and seasonal changes. Thus, higher temperatures in the Mediterranean region associated to global warming may affect any of these processes and, consequently, olive production in the near future. Despite the importance of this issue, there is not much information on this respect.

In the northern hemisphere two vegetative growth flushes can be observed: the main one from March to mid-July and the second from September to mid-October provided that water is not a limiting factor. The optimum temperature for olive shoot growth and development ranges from 10 to 30 °C, but when temperature rises above 35 °C shoot growth could be limited (Rallo and Cuevas, 2008; Therios, 2009). This effect has been recently observed in different olive plant material when plants were exposed to moderately high temperature (37 °C) during a period of time (Benlloch-González et al., 2016, 2017). From this information, it is not clear in which sense the change in temperature patterns along the year, especially during winter and autumn, will affect the vegetative growth in this species.

Most of the available information on the potential effects of warmer temperature on olive fruitfulness has been focused on floral phenology, paying little attention on the following reproductive processes. Regional Climate Models and olive-pollen capture traps studies, have informed that the development of flower structures will be completed faster leading to earlier flowering dates (García-Mozo et al., 2010;

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Oteros et al., 2013; Osborne et al., 2000; Giannakopoulos et al., 2009; Orlandi et al., 2010; Aguilera et al., 2015). An advance in the flowering date has been also observed in a recent study in which olive trees growing under field conditions were exposed during three consecutive years to 4 °C above the ambient temperature using temperature controlled open-top-chambers (Benlloch-González et al., 2018). In addition, the higher temperature affected floral differentiation, favoring pistil abortion, and fertilization processes leading to a reduction in fruit set (Benlloch-González et al., 2018).

After fruit set, olive growth and development are completed in approximately 4–5 months, following a double sigmoid growth curve pattern (Hartmann, 1949; Lavee, 1996; Rallo and Cuevas, 2008). During this period structural changes and chemical transformations such as cell division, cell expansion and storage of metabolites, take place in the different fruit tissues. Phase I is characterized by an exponential growth. During this phase, cellular divisions of the different fruit tissues are predominant, the mesocarp and the endocarp increase in size. The sclerification and hardening of the endocarp begin. In phase II, fruit growth slows down or stops, the embryo and the endocarp reach their final size and the endocarp hardening process is completed. During phase III, there is a fast growth of the fruit due to the enlargement of the mesocarp cells which determines the final fruit size. Lipogenesis in flesh parenchyma cells begins (Manrique et al., 1999). This phase ends in early autumn when fruit undergoes the first pigmentation changes.

All these processes are genetically controlled and influenced by several environmental factors (Connor and Fereres, 2005; Costagli et al., 2003; Gucci et al., 2009), being water availability the most studied. When water shortage occurs at phase I, smaller endocarps are observed (Lavee, 1986) which can lead to fruits with unusually high pulp/stone ratios compromising fruit viability. Moreover, water reduction during this stage has been informed to affect cell size rather than cell number in the mesocarp (Rapoport et al., 2004). Water availability in phase III determines the final size of the fruit and its oil content. Limitation of water during this period results in small fruits with reduced oil content (Beltrán et al., 2004). Although water limitation effects on fruit development and growth have been well described, the information related to higher temperature is scarce. There is some information from studies performed in the southern hemisphere, in which the effect of warmer temperatures has been analysed on fruit dry weight, oil concentration, and oil fatty acid composition. Fruiting branches from 'Arauco' olive cultivar were enclosed in transparent plastic chambers with individualized temperature control during the oil accumulation phase (García-Inza et al., 2014, 2018). Under these experimental conditions, temperatures above 25 °C reduced fruit fresh weight. A reduction in fruit oil concentration was also observed when temperature was increased during the period of active oil accumulation.

During the ripening process, the fruit darkens from lime-green to purple-black at the same time that oil content increases. The purple or black colour of the fruit is due to the formation of anthocyanins (Roca and Minguez-Mosquera, 2001). The amount of anthocyanins in a fruit determines its color and depends on its biosynthesis, accumulation and degradation. Temperature influences these processes. High temperature has been described to reduces anthocyanins accumulation in many fruits and plant tissues (Steyn et al., 2002) affecting fruit color (Koshita, 2015). This has been observed in different fruit species such as grapes (Tomana et al., 1979; Naito et al., 1986), apple (Creasy, 1968; Yamada et al., 1988; Arakawa, 1991), Satsuma mandarin (Utsonomiya et al., 1982), and Japanese persimmons (Taira et al., 2000; Isobe and Kamada, 2001), but it is not clear in olive fruit. The final changes in fruit colouring is an important stage during the olive fruit maturation after which oil accumulation processes are ceased (Lavee and Wodner, 1991).

In order to elucidate how global warming will affect olive maturation and yield as well as vegetative growth, a field study with the cultivar 'Picual' has been carried out in a Mediterranean climate type area. Trees were subjected to warmer temperature than ambient throughout their complete reproductive cycle using temperature-controlled open-top-chambers (OTCs). The impact of high temperature on fruit growth and development, maturation period, ripening processes, oil production and yield has been analyzed. The information from this study along with a previous one (Benlloch-González et al., 2018), gives an important overview of olive production associated to global warming.

2. Material and methods

2.1. Plant material and growth conditions

'Picual' olive trees (*Olea europaea* L.) growing in the experimental farm of 'Campus de Rabanales', University of Córdoba, Spain (37°55′N 4°43′W) were used to perform the experiment. The orchard soil is classified as Calcic Luvisols with a clay-loam to clay texture, pH moderately alkaline (7–8), organic matter around 2%, and moderate to high cation exchange capacity (Del Campillo et al., 1993). The trees were planted in autumn 2009 spaced 8 x 6 m apart, with a drip irrigation system. Depending on the season, water was applied over five to six months during the dry season (from late May to middle October, approximately). During this period the dose applied was about 55.2 l per tree and day. The experiment was conducted from 2014 to 2017.

2.2. Temperature treatments

Sixteen trees, consecutively distributed in two lines, were selected from the experimental orchard to perform this study. Trees were subjected permanently to two temperature treatments, ambient temperature (AT) and 4 °C above ambient temperature (AT + 4°C), during three consecutive years (2014–2017). To increase the ambient temperature in 4 °C, temperature-controlled open-top-chamber (OTC) systems were used. Each OTC, containing a single tree, was equipped with heating and ventilation devices regulated by an automaton to maintain a constant day/night temperature gradient between the tree and the surrounding environment of 4 °C throughout the complete reproductive cycle of this species. Further details about the functioning of this system have been described in Benlloch-González et al. (2018). The experimental design consisted of four blocks, each one with the two temperature treatments (TA; TA + 4°C) randomly distributed.

2.3. Measurements

Vegetative growth (shoot length, trunk diameter and weight of the pruning material) was measured once a year at the end of the vegetative period (late Autumn). Shoot length was measured on fifteen uniformly distributed shoots per tree, which were previously selected and tagged each spring. After harvesting, the trees were pruned and the trunk circumference measured at 30 cm above the ground surface.

To determine the fruit maturation period, the experimental trees were visited every 3–4 days from late August to December, recording the fruit phenological stages of each tree according to the following visual scale: 1 deep green skin; 2 yellowish-green skin; 3 veraison, green skin with reddish patches over more than half of the fruit; 4 purple skin; 5 black skin and white flesh. The maturation period was determined according to Barranco et al. (1998).

At harvest, fruits of each tree were collected to determine total weight. Fifty to eighty fruits per tree, depending on the year, were used to determine fruit size (average weight of the fruits sampled), pulp/stone ratio, expressed as fresh weight, and the maturity index (MI). The MI was determined according to Ferreira (1979). The fruits were classified into 8 categories (1–8) according to the visual scale mentioned above (1–5) extended to 3 more categories: 6 black skin and purple pulp over less than half of the pulp; 7 black skin and purple pulp not reaching the stone but covering more than half of the pulp, and 8 black

skin and purple pulp up to the stone. MI is the sum of the multiplication of the number of fruits in each category by the numerical value of each category, divided by total number of fruits.

Fruit oil content was determined by nuclear magnetic resonance (NMR) (Minispec mq 20, Bruker Analytik Gmbh). The results were expressed as percentage of fresh and dry weight (% FW and DW). Anthocyanin fraction was extracted from olive pulp using extraction methods described by Lee et al. (2005) with some modifications. Total anthocyanin content of diluted fruit extract was estimated by the pH differential spectroscopic method proposed by Cheng and Breen (1991). Absorbance (A) was measured with a UV–vis spectrophotometer at 510 nm and 700 nm in diluted buffers at pH 1 and pH 4.5, where $A = (A_{510}\text{-}A_{700})_{pH\ 1} - (A_{510}\text{-}A_{700})_{pH\ 4.5}$. Data was expressed as cyanidin-3-glucoside equivalent per kg of fresh weight. The extraction of the phenolic fraction from the pulp was carried out following the method proposed by Gómez-Rico et al. (2008). Total polyphenols content was determined by the colorimetric method described by Vázquez-Roncero et al. (1973), using the reagent Folin–Ciocalteu. Absorbance was measured with a UV–vis spectrophotometer (CaryBio50, Varian) at 725 nm. Results were expressed as mg of caffeic acid per kg of pulp.

2.4. Statistical analysis

Analyses of variance were performed on the data using Statistix 9.0 software package (Analytical Software, Tallahassee, FL, USA). In all analyses, residual plots were generated to identify outliers and to confirm that variance was common and normally distributed. All percentages values were transformed using the arcsin of the square root before analysis.

3. Results

Under the experimental conditions of this study, a relatively constant temperature gradient of 4 °C between ambient trees (AT) and trees inside the temperature-controlled open-top-chambers (AT + 4°C), was maintained along three consecutive reproductive cycles (2015–2017) (Fig. 1). This data shows that the experimental system used to subject trees, growing under field conditions, to warmer temperatures than ambient is a reliable method.

The increase of ambient temperature in 4 °C (AT + 4°C) affected the vegetative growth of trees (Table 1). There was no effect of this treatment on the growth of tagged shoots in 2015 and 2016, but there were significant differences in 2017. The trunk diameter (cm) of tress at the beginning of the experiment was similar [7.3 (AT) vs. 7.4 (AT + 4°C)]. However, after exposing trees to 4 °C above ambient temperature differences were observed. The increment (Δ) of the trunk diameter was significantly greater in AT + 4°C than in AT trees at the end of each growing season (2015–2017). The same tendency was observed with the pruning material. This is, 4 °C above ambient temperature applied constantly along the three growing seasons, promoted the vegetative growth of AT + 4°C trees resulting in trees of significantly bigger size (Table 1).

The fruit maturation period, i.e., days from the start of veraison to ripeness, was also affected by temperature (Fig. 2). The appearance of reddish spots in the fruits was forwarded about 17–30 days in trees subjected to high temperature (AT + 4°C) when compared with AT trees. This effect was periodically observed in 2015–2017 interval. In addition, the warmer temperature prolonged the maturation period in 2015 and 2016 while no effect was observed in 2017 (Fig. 2).

Although fruit yield in trees growing under ambient temperature (AT) was not very high, it was significantly affected in AT + 4°C trees due to the temperature treatment applied during the complete reproductive cycle of the trees (Table 2). It was highly impacted in 2015 and in less but similar proportion in 2016 and 2017 (about 60–70% of reduction, respectively). Fruit oil content values, expressed as percentage of dry and fresh fruit weight (% DW and FW), were also

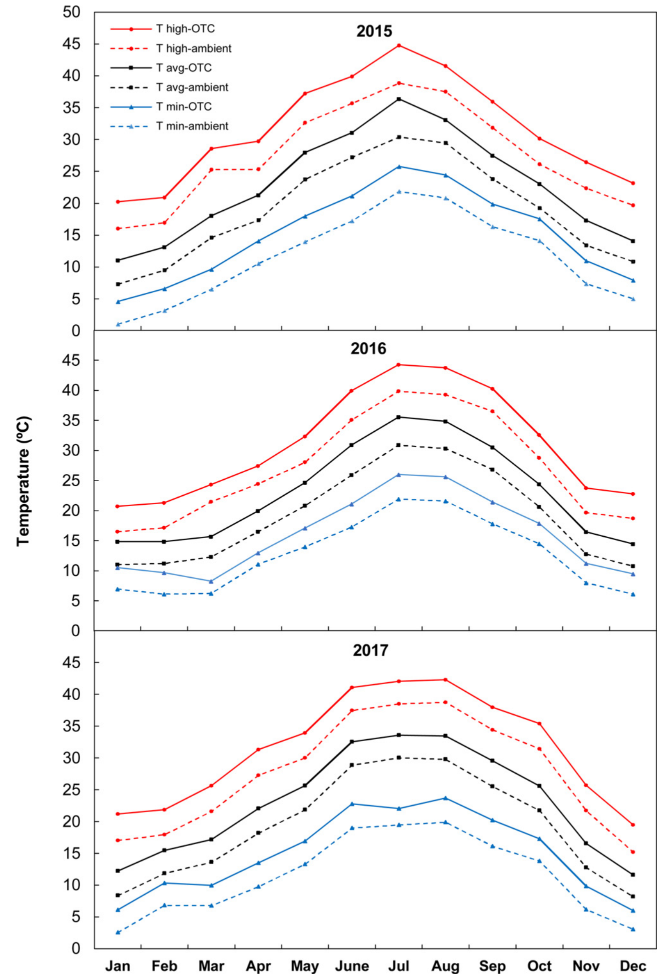

Fig. 1. Average monthly temperatures recorded from January to December during three consecutive years (T_{avg}). Dotted lines show ambient temperatures and the straight lines show OTC temperatures. T_{high} and T_{low} represents average of daily high and low temperatures by month respectively.

significantly lower in those trees subjected to warmer temperatures (AT + 4 °C vs. AT) (Table 2). The reduction in fruit oil content by the high temperature treatment was similar (about 30% compared to AT trees) along the tree years when expressed over FW. While it was expressed over DW this effect was more marked in 2015 than in 2016 and 2017 (about 33 and 20% of reduction, respectively).

At harvest, differences in fruit characteristics were observed between temperature treatments (AT vs. AT + 4°C) (Table 3). Fruits size was reduced by the AT + 4°C treatment in 2015 and 2016. In 2017 fruits grown under ambient temperature (AT) were smaller in size when compared with those of previous growing seasons and no effect was observed due to the AT + 4°C treatment. Pulp/stone ratio was smaller in AT + 4°C fruits than in AT ones in all seasons. There were no differences in maturity index (MI) between treatments in 2015. However, it was lowered by the AT + 4°C temperature treatment in 2016 and 2017 seasons (Table 3).

The accumulation of anthocyanins in fruits during the maturity period was significantly different in AT and AT + 4°C trees (Table 4). Greater values were observed in fruits of AT trees in all seasons, this is, warmer temperatures during this period decreased the accumulation of anthocyanins in fruits of AT + 4°C trees. There were no differences in fruit polyphenols contents between treatments in 2016. The high temperature treatment decreased fruit polyphenols content in 2017 (Table 4).

Table 1
Effect of a 4 ºC increase in ambient temperature (AT vs. AT + 4ºC) on vegetative growth.

Temperature treatment	Vegetative growth[1,2]								
	2015			2016			2017		
	Shoot growth (cm)	Trunk diameter[3] (cm)	Pruning material (kg)	Shoot growth (cm)	Trunk diameter (cm)	Pruning material (kg)	Shoot growth (cm)	Trunk diameter (cm)	Pruning material (kg)
AT	1,6 a	8,1 (0,8) b	4,2 b	9,8 a	9,4 (1,3) b	4,9 b	4,8 b	10,6 (1,2) b	3,9 b
AT + 4°C	1,4 a	8,7 (1,3) a	8,1 a	11,2 a	10,7 (2,0) a	11,0 a	7,6 a	12,5 (1,8) a	12,6 a
[4]*CV (%)*	*31.0*	20.7	*31.9*	*14.0*	*12.5*	*37.5*	*21.3*	*18.6*	*25.9*

[1] Means within each column followed by different letters are significantly different at P ≤ 0.05 by F-test.
[2] Each data is the mean of eight trees. In the case of shoot growth, it was obtained from 15 vegetative shoots per tree.
[3] Numbers in parenthesis are the increment of the trunk diameter of trees in two consecutive years.
[4] Coefficient of Variation.

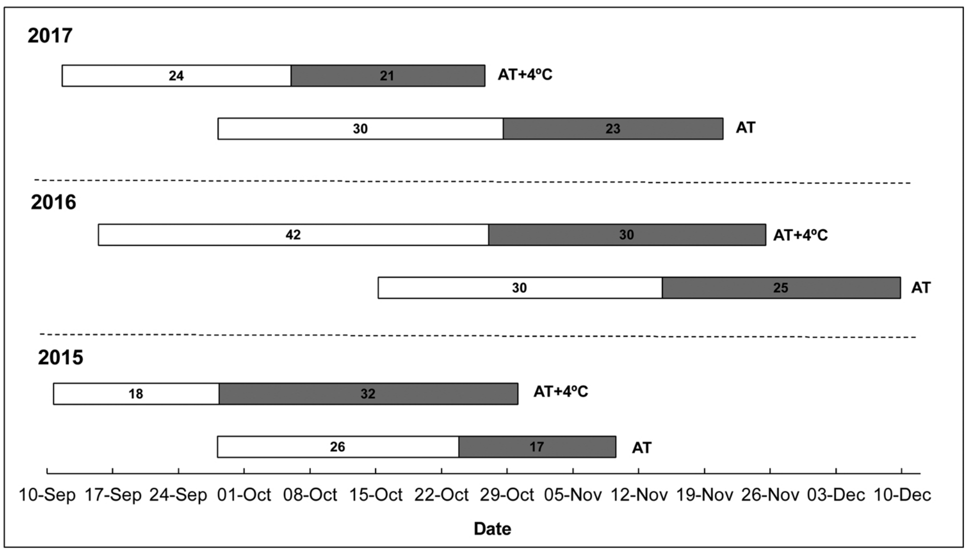

Fig. 2. Fruit maturation period under ambient temperature (AT) and 4 °C above ambient temperature (AT + 4°C) in three consecutive years. Inside each bar from left to right are represented the periods of time (days) from the start to the end of veraison and from the end of veraison to ripeness.

Table 2
Effect of a 4 °C increase in ambient temperature (AT vs. AT + 4°C) on fruit yield and oil content.

Temperature treatment	2015			2016			2017		
	Fruit yield (kg per tree)	Oil content		Fruit yield (kg per tree)	Oil content		Fruit yield (kg per tree)	Oil content	
		(%DW)	(%FW)		(%DW)	(%FW)		(%DW)	(%FW)
AT	5,1 a	53,7 a	18,1 a	16,7 a	52,1 a	19,1 a	22,4 a	51,2 a	20,6 a
AT + 4°C	0,4 b	35,7 b	12,3 b	6,6 b	42,0 b	12,7 b	6,8 b	39,9 b	14,2 b
[1]*CV (%)*	*61.23*	*23.86*	*14.43*	*39.39*	*3.93*	*8.59*	*25.08*	*9.56*	*5.73*

Means within each column followed by different letters are significantly different at P ≤ 0.05 by F-test.
Each data is the mean of eight trees.
[1] Coefficient of Variation.

4. Discussion

In a previous work (Benlloch-González et al., 2018) we presented the results of this experiment relative to the effect of high temperature on flowering and fruit set processes. It was emphasized that in other studies the effect of global warming was analyzed contrasting the behavior of crops located in regions with different mean temperatures or developing models to predict the performance of a particular crop (De Melo-Abreu et al., 2004; Giannakopoulos et al., 2009; Orlandi et al., 2014; El Yaacoubi et al., 2014; Gabaldón-Leal et al., 2017). In our study we evaluated the effect of global warming on the olive installing temperature-OTC systems under field conditions in an area vulnerable to climatic changes in the near future (Giorgi, 2006; Lionello, 2012; IPCC, 2014). The accuracy of the system is shown in Fig. 1.

In the above-mentioned study, we concluded that if temperature increases 4 °C above the ambient temperature in this region, olive flowering would be advanced and last longer, significantly increase pistil abortion leading to a reduction in fruit set. Results presented in the present work were obtained from the same experimental trees along the same years. Consequently, they show the end of the fruiting cycle of these trees. The reduction in fruit set, led to a significant reduction in fruit yield, but also in oil content. A reduction in fruit yield usually led

Table 3
Effect of a 4 ºC increase in ambient temperature (AT vs. AT + 4ºC) on fruit size, pulp/stone ratio and maturity index (MI).

Temperature treatment	Fruit characteristics[1,2]								
	2015			2016			2017		
	Fruit size (g/fruit)	Pulp/stone	MI	Fruit size (g/fruit)	Pulp/stone	MI	Fruit size (g/fruit)	Pulp/stone	MI
AT	5,7 a	9,0 a	3,9 a	5,5 a	8,3 a	4,3 a	4,5 a	9,2 a	4,7 a
AT + 4°C	3,3 b	4,9 b	3,8 a	5,1 b	7,1 b	4,0 b	4,8 a	6,9 b	4,0 b
[3]*CV (%)*	*15.15*	*15.84*	*9.42*	*3,35*	*8,20*	*4,71*	*14,56*	*12,53*	*7,93*

[1] Means within each column followed by different letters are significantly different at $P \leq 0.05$ by F-test.
[2] Each data is the mean of eight trees and was obtained from 50 fruits per tree.
[3] Coefficient of Variation.

Table 4
Effect of a 4 ºC increase in ambient temperature (AT vs. AT + 4ºC) on fruit anthocyanins and polyphenols content.

Temperature treatment	2015		2016		2017	
	Anthocyanins (cyanidin-3-glucoside equivalent kg^{-1} FW)	Polyphenols (mg caffeic acid kg^{-1} pulp)	Anthocyanins (cyanidin-3-glucoside equivalent kg^{-1} FW)	Polyphenols (mg caffeic acid kg^{-1} pulp)	Anthocyanins (cyanidin-3-glucoside equivalent kg^{-1} FW)	Polyphenols (mg caffeic acid kg^{-1} pulp)
AT	192,6 a	–	993,9 a	8726 a	293,4 a	9511,2 a
AT + 4°C	106,4 b	–	490,5 b	11482 a	127,2 b	6347,6 b
[1]*CV (%)*	*21.75*		*12.91*	*12.21*	*33.33*	*11,05*

Means within each column followed by different letters are significantly different at $P \leq 0.05$ by F-test.
Each data is the mean of eight trees.
[1] Coefficient of Variation.

to an increase in fruit size. This phenomenon is common in fruit tree species, including the olive and, in fact, fruit thinning is done to increase fruit size at harvest in apple, peaches, and other fruit tree species (Dennis, 2000; Looney, 1993; Wertheim, 2000; Costa and Vizzotto, 2000). However, in our study fruit size was smaller in AT + 4°C than in AT trees, even when fruit yield was significantly lower. Yield, fruit size and oil content depend on both genetic and environmental conditions (Lavee and Wodner, 1991). Despite that olive is well adapted to adverse environmental conditions, water stress along the different stages of fruit growth and maturity have been reported to highly affect those parameters (Lavee, 1996). Fruit size has been described to be reduced when water deficit is applied during early fruit growth (Rapoport et al., 2004; Gucci et al., 2009). This effect was mainly attributed to a failure in mesocarp cells extension rather than division. If water limitation is constant along the dry season, the metabolic activity is slowed down and consequently fruit growth and oil accumulation reduced (Lavee, 1996). When occurring at the end of the dry season, when fruit growth rate and oil production are intense, fruits of smaller size and lower oil content are produced. The results obtained under the experimental conditions of the present study could be explained by a water stress effect associated to a higher evotranspiration demand of trees due to elevated temperature inside the open-top-chamber during the dry season. From the results of this study we cannot elucidate what stage of fruit growth and maturity was more sensitive to the high temperature treatment, but it is clear that it affects any of the developmental processes that determine final fruit size and oil accumulation. Although studies performed in the southern hemisphere with the cultivar 'Arauco' have observed a reduction in fruit size and oil content when high temperature was applied during the oil accumulation phase (García-Inza et al., 2014, 2018), there is not much information on how global warming will affect these parameters increasing the need of further research on this respect.

During fruit maturation changes in fruit color occur at the same time that oil content increases. In our study the fruit maturity period was forwarded and extended in AT + 4°C trees. Therefore, the reduction in oil content could be also due to a delay in lipogenesis because of the delay in fruit maturation. In fact, the maturity index indicates that the trees subjected to higher temperatures at the time of harvest showed a lower MI than those growing at ambient temperatures. Also, anthocyanins found in AT + 4°C trees, a flavonoid responsible of the fruit color in the olive fruit, was significantly lower than in AT trees, supporting the delay in fruit maturation. This reduction in fruit anthocyanins content due to high temperature has been observed for long in other species (Utsonomiya et al., 1982; Naito et al., 1986; Yamada et al., 1988; Arakawa, 1991; Taira et al., 2000; Isobe and Kamada, 2001). The same effects on fruit maturation were observed in trees subjected to high doses of nitrogen (Fernández-Escobar et al., 2014), indicating the relationships between those effects.

Olive trees grow, as most woody species, by forming new shoots and extending the old ones, and by thickening those formed. A measure of each defines the annual growth of the tree and tree size. In this experiment, vegetative growth was exuberant in AT + 4°C trees. The annual growth of the trees, estimated measuring shoot growth at the end of the vegetative period and by the weight of the pruning material, was higher in AT + 4°C than in AT trees, probably because of the stimulative effect of temperature (Way and Oren, 2010). Trunk girth has been related to tree weight (Westwood, 1993) and, consequently, is an estimation of tree size (Fernández-Escobar, 2014). In our work, trunk diameter was higher in AT + 4°C trees, suggesting that the effect of higher temperatures have a direct effect on olive tree growth. The lower temperature threshold for olive vegetative and trunk growth has been estimated to be around 15 and 7 °C respectively (Pérez-López et al., 2008). So it seems that warmer temperatures during winter and autumn prolonged the growing season in AT + 4°C trees resulting in an increase in tree size.

In conclusion, increasing temperature 4 °C above the actual ambient temperature could lead to 1) a delay in fruit maturation, reducing oil content because a delay in lipogenesis, 2) fruit of smaller size, 3) a reduction in yield, due to a reduction in fruit set and an increase in pistil abortion, and 4) an increase in the size of trees. These results suggest that under future warmer conditions, plantation density must be lower to prevent interferences between nearby trees. In addition, actual irrigation management practices should be revised to reduce pistil abortion and increase fruit size and, consequently, yield.

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